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AVIAN HABITAT RELATIONSHIPS IN PINYON-JUNIPER WOODLAND

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ABSTRACT.—Habitat relationships of breeding birds were examined in northwestern Colorado in pinyon-juniper (*Pinus edulis-Juniperus osteosperma*) woodland and in openings where most overstory trees had been knocked down by anchor chaining. Vegetation characteristics and physical habitat features were measured in 233 0.04-ha circular plots around singing males of 13 species of birds from 15 May to 15 July 1980. Thirteen-group discriminant function analysis ordinated bird species along three habitat dimensions described by (1) canopy height; (2) slope, shrub size, and shrub species diversity; and (3) percentage canopy cover, large tree density, distance from a habitat edge, litter cover, and green cover. Woodland, open-area, and intermediate edge species were clearly segregated along the first discriminant axis, and species' associations with shrubs, inclination, ground cover, and edges were revealed by the ordinations along the second and third discriminant axes. Two-group discriminant analyses comparing occupied and available plots identified additional and more specific habitat associations. For example, Hermit Thrushes (*Catharus guttatus*) were associated with mature forested habitats and forest interiors, Virginia's Warblers (*Vermivora virginiae*) favored steep, oak-covered draws, Rock Wrens (*Salpinctes obsoletus*) selected areas where percentage log cover and small tree density were high, and Dusky Flycatchers (*Empidonax oberholseri*) preferred shrubby slopes with scattered large trees near woodland edges. *Received 28 Aug. 1986, accepted 15 Jan. 1987.*

Pinyon-juniper woodland is one of the most expansive plant communities in the U.S., occupying some 172,000 km^2 of land (Clary 1975). It dominates much of the landscape in the Southwest, and in New Mexico it occupies 26% of the land surface (Pieper 1977). Because of its relatively low commercial value, vast areas have been converted to grazing lands, especially since 1950, by removing overstory trees. Chaining has been the most widely used conversion technique and involves dragging an 80–200-m anchor chain (20–40 kg/link) between 2 bulldozers, which knocks down the trees (Aro 1975).

Despite the expansiveness and rapid type-conversion of pinyon-juniper woodlands, these areas have been largely ignored by avian ecologists. Balda and Masters (1980) provided an overview of the ecology of the avifauna, and others have examined the effects of type-conversion on breeding birds (O'Meara et al. 1981, Sedgwick and Ryder 1986). Limited information exists, however, on the habitat relationships of songbirds breeding in pinyon-juniper woodlands. This study identifies habitat as-

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sociations of breeding birds in pinyon-juniper woodland, including woodland where most of the trees had been knocked down by chaining.

STUDY AREA

The study was conducted in northwestern Colorado in the Piceance Basin, an area ranging from 1737 to 2590 m in elevation. The dominant overstory vegetation in the area is pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*). Low elevation woodlands on shales are dominated by juniper with an understory of scattered prairie junegrass (*Koleria cristata*), bluebunch wheatgrass (*Agropyron spicatum*), needle-and-thread (*Stipa comata*), bottlebrush squirreltail (*Sitanion hystrix*), Indian ricegrass (*Oryzopsis hymenoides*), and sometimes stunted antelope bitterbrush (*Purshia tridentata*) and true mountainmahogany (*Cercocarpus montanus*). Common forbs include groundsel (*Senecio* spp.), skyrocket gilia (*Gilia aggregata*), penstemon (*Penstemon* spp.), Hood phlox (*Phlox hoodii*), and Nuttall golden weed (*Haplopappus nuttallii*). Pinyon pine, big sagebrush (*Artemisia tridentata*), and western wheatgrass (*A. smithii*) join on sandstone to form a more diverse plant community. Above 2100 m, pinyon pine dominates the overstory, and the shrub layer is composed of big sagebrush, rabbitbrush (*Chrysothamnus* spp.), antelope bitterbrush, and occasionally true mountainmahogany, common chokecherry (*Prunus virginiana*), and Saskatoon serviceberry (*Amelanchier alnifolia*). Gambel oak (*Quercus gambelii*) is prominent on steep slopes and frequently occurs in shady ravines. The grass-forb community above 2100 m includes most species found at lower elevations, but percentage ground cover is higher; arrowleaf balsamroot (*Balsamorhiza sagittata*) and lupine (*Lupinus* spp.) are also frequently present.

I collected data over the entire range of environmental variation in the pinyon-juniper type. This included both undisturbed pinyon-juniper habitat and openings created by chaining. Study sites included (1) xeric, low-elevation stands of nearly pure juniper; (2) shrub-dominated stands with only scattered pines and junipers; (3) mesic, high-elevation stands dominated by pinyon pines; and (4) chainings that varied in age from 4–17 years and in size from 0.2 to 7 km^2.

METHODS

Habitat selection was studied from 15 May to 15 July 1980. Singing males encountered while walking through chained and unchained pinyon-juniper woodland were considered as centers of 0.04-ha circular plots within which vegetation was sampled. Such plots are thought to be representative of the breeding habitat of many species of birds (James 1971, Smith 1977). I used modifications of sampling techniques described by James and Shugart (1970) and Shugart and Patten (1972). Determinations of canopy cover and several categories of ground cover were made while pacing along each of four randomly oriented, orthogonal transects (radii) in each circular plot. By sighting directly upward through an ocular tube on alternate steps, limbs or green vegetation were considered as positive scores for canopy cover. Similarly, presence of bare ground, forb cover, grass cover, shrub cover, litter cover, and log cover were determined by sighting downward through the tube about 1 m in front of the observer. A cover type sighted through the cross hairs of the ocular tube was considered a positive score. Twenty sightings for canopy cover and 20 for ground cover were made in each circular plot. Using a Biltmore "reach stick" (Forbes 1955), I determined live tree density by counting the number of trees in each of 9 diameter-at-breast-height (dbh) size classes. I used the Bitterlich variable radius technique to determine basal areas of dead, live, and "part" live trees (trees with ≥25% dead limbs) by species (Grosenbaugh 1952). A measure of openness of the habitat was determined by counting the number of quadrants in each circle without trees. The point-centered quarter method (Cottam and Curtis 1956) was used to determine shrub density. I measured canopy height using triangulation techniques (Whitmore 1975) and estimated slope to the nearest five degrees. Slope orientation was derived after the method of Smith (1977). In all, 39 measured and created variables were used in the analysis (Table 1).

Analytical techniques.—Stepwise descriptive discriminant analysis (DDA) (Williams 1983) was used to ordinate bird species along dimensions of habitat and to describe species-species relationships in the context of habitat. DDA attempts to distinguish statistically (discriminate) between two or more groups (species of birds) by forming linear, additive combinations of variables on which the groups are expected to differ (quantitative measures of habitat). A 13-group DDA was performed on a data set which included 13 species of birds (N = 233), each with a sample size ≥10 (Table 2). A stepwise variable entry technique selected the "best set" of habitat variables and reduced the complexity of the original variable set. Discriminant scores were determined for each observation by summing the products of the coefficients and the values of their associated variables. Bird species were ordinated along the discriminant functions according to their mean discriminant scores. Confidence ellipses of species' bivariate means for the first two discriminant functions were computed using the technique of Sokal and Rohlf (1969).

Stepwise 2-group DDA was performed for each of the 13 bird species, comparing sites occupied by each species with the pooled set of sites occupied by all remaining species. I considered the sites occupied by all other species as available habitat. This analysis puts emphasis on individual species-habitat relationships and provides a better resolution of species-specific habitat requirements (Conner et al. 1983). Thirteen separate DDAs were performed, one for each species.

Predictive discriminant analysis (PDA) (Williams 1983) was used to provide an empirical test of the discriminating power of the variables selected by DDA and to provide additional insight into habitat selection and habitat segregation. PDA derives a set of functions (one for each species) that classify observations (habitat information from the circular plots) into groups (bird species). The Statistical Program for the Social

TABLE 1

DESCRIPTIONS OF THE MEASURED AND DERIVED VARIABLES USED IN HABITAT SELECTION ANALYSES, PICEANCE BASIN, 1980

Mnemonic	Description
ALT	Altitude (m)
BITPL	Basal area of live pinyons (using Bitterlich method)
BITJL	Basal area of live junipers
BITOL	Basal area of live oaks
BITLIVE	BITPL + BITJL + BITOL
BITPD	Basal area of dead pinyons
BITJD	Basal area of dead junipers
BITDEAD	BITPD + BITJD
BITPP	Basal area of live pinyons with ≥25% dead limbs
BITJP	Basal area of live junipers with ≥25% dead limbs
BITPART	BITPP + BITJP
BITALL	BITLIVE + BITDEAD + BITPART
BITZERO	Number of quadrants of 0.04-ha circle without trees
CANHT	Canopy height (m)
DENSTYA	Tree density (dbh = 0–15.2 cm)
DENSTYB	Tree density (dbh = 15.2–22.9 cm)
DENSTYC	Tree density (dbh = 22.9–38.1 cm)
DENSTYD	Tree density (dbh = 38.1–53.3 cm)
DENSTYE	Tree density (dbh = 53.3–68.6 cm)
DENSTYF	Tree density (dbh = 68.6–83.8 cm)
DENSTYG	Tree density (dbh = 83.8–101.6 cm)
DENSTYH	Tree density (dbh = 101.6–119.4 cm)
DENSTYI	Tree density (dbh > 119.4 cm)
EDGDIST	Distance (m) to a habitat edge
EWDIREC	East-west slope orientation
GRNDSP	Number of forb and grass species in 0.04-ha circle
NSDIREC	North-south slope orientation
PBARE	Percentage bare ground
PCANOPY	Percentage canopy cover
PCOVER	Percentage ground cover (includes grass, forbs)
PDEADTR	Percentage dead trees (BITDEAD/BITALL)
PGCOVER	Percentage green cover (grass, forbs, and shrubs)
PLITTER	Percentage litter cover
PLOG	Percentage log cover (includes chaining debris)
SHRBHT	Mean shrub height
SHRBDIM	Mean shrub diameter
SHRUBSP	Number of shrub species in 0.04-ha circle
SHRBDEN	Shrub density
SLOPE	Estimate of ground slope (to nearest 5°)

TABLE 2

BIRD SPECIES SEEN ON THE STUDY AREA AND USED IN THE DISCRIMINANT ANALYSES

Mnemonic	N	Species
MD	14	Mourning Dove (*Zenaida macroura*)
DF	11	Dusky Flycatcher (*Empidonax oberholseri*)
RW	18	Rock Wren (*Salpinctes obsoletus*)
HT	10	Hermit Thrush (*Catharus guttatus*)
BGG	20	Blue-gray Gnatcatcher (*Polioptila caerulea*)
SV	13	Solitary Vireo (*Vireo solitarius*)
VW	15	Virginia's Warbler (*Vermivora virginiae*)
BTG	28	Black-throated Gray Warbler (*Dendroica nigrescens*)
GTT	30	Green-tailed Towhee (*Pipilo chlorurus*)
RST	20	Rufous-sided Towhee (*P. erythrophthalmus*)
VS	17	Vesper Sparrow (*Pooecetes gramineus*)
CS	18	Chipping Sparrow (*Spizella passerina*)
BS	19	Brewer's Sparrow (*S. breweri*)

Sciences computer package (SPSS, Version 8) was used for all analyses (Nie et al. 1975).

RESULTS AND DISCUSSION

Thirteen-Group DDA.—Seventeen of the original 39 variables were selected by DDA for discriminating among the 13 species of birds. Three discriminant functions explaining 78.0% of the among-species variance had significant discriminating power ($P < 0.01$) and were ecologically interpretable (Table 3). The first function explained >50% of the among-species variance; canopy height (CANHT), with a coefficient of 0.65, was the dominant variable in discriminant function 1 (DF1). This function may be interpreted as a dimension of trees, representing a continuum from an open, treeless situation to one where large, mature trees are predominant. Bird species occurring in open areas would be expected to have low discriminant scores, and species found in mature pinyon-juniper should have high scores for this function. Discriminant function 2 (DF2) explained an additional 17% of the available discriminating information, and showed a heavy weighting on slope, shrub species richness (SHRBSP), and shrub size (SHRBHT). This function described a gradient from a relatively flat situation, where shrubs were small and shrub species richness was low, to one where shrubs, especially large shrubs on slopes, were predominant. DF3 explained 10% of the discriminating information and contrasted large trees (DENSTYE), percentage canopy cover (PCANOPY), and distance from a habitat edge (EDGDIST) with percentage litter

TABLE 3
SUMMARY OF THE 13-GROUP DISCRIMINANT ANALYSIS

Variable	Discriminant function coefficients[a]		
	Function 1	Function 2	Function 3
CANHT	−0.65	0.08	0.13
PCANOPY	−0.07	−0.32	−0.71
PGCOVER	−0.19	0.36	0.53
PLITTER	−0.21	−0.04	0.50
PBARE	−0.17	0.42	0.34
PDEADTR	−0.11	0.27	−0.15
BITJD	−0.06	−0.07	0.23
DENSTYA	0.23	0.06	−0.15
DENSTYB	−0.23	0.28	0.10
DENSTYE	−0.13	−0.03	−0.53
DENSTYI	0.04	0.22	0.02
SHRUBSP	0.08	−0.64	0.19
SHRUBHT	0.02	−0.45	−0.28
EDGDIST	0.05	−0.37	−0.53
SLOPE	−0.29	−0.62	0.13
ALT	−0.28	0.41	0.27
EWDIREC	−0.19	0.24	0.17
% variance explained[b]	50.4	17.3	10.3
Cumulative % variance explained	50.4	67.7	78.0

[a] Coefficients indicate relative contributions of the variables to each function.
[b] Percentage variance indicates the amount of the among-groups variance accounted for by each function.

(PLITTER) and percentage green cover (PGCOVER). Thus, this function described a gradient going from grassy, shrubby situations to those where a habitat edge was distant, large trees were dominant, and percentage canopy cover was high.

Species associated with open areas versus those from woodland habitats were clearly separated along DF1 (Fig. 1). Hermit Thrush (see Table 2 for scientific names) and Solitary Vireo, for example, which occurred only in mature woodland, lay farthest to the left along DF1, whereas species associated with chainings or natural openings in pinyon-juniper (e.g., Brewer's Sparrow, Rock Wren) were farthest to the right. Chipping Sparrow, often associated with pinyon-juniper edges, was midway along the axis ranging from "openness" to "trees." Virginia's Warbler, Dusky Flycatcher, and Rufous-sided Towhee were often found on steep slopes where shrub cover was high and these species had the lowest scores along DF2. At the opposite end of DF2 were Chipping Sparrow and Vesper Sparrow which occurred in flatter areas where shrubs were smaller and less diverse. Hermit Thrush preferred interior woodlands and had the lowest score

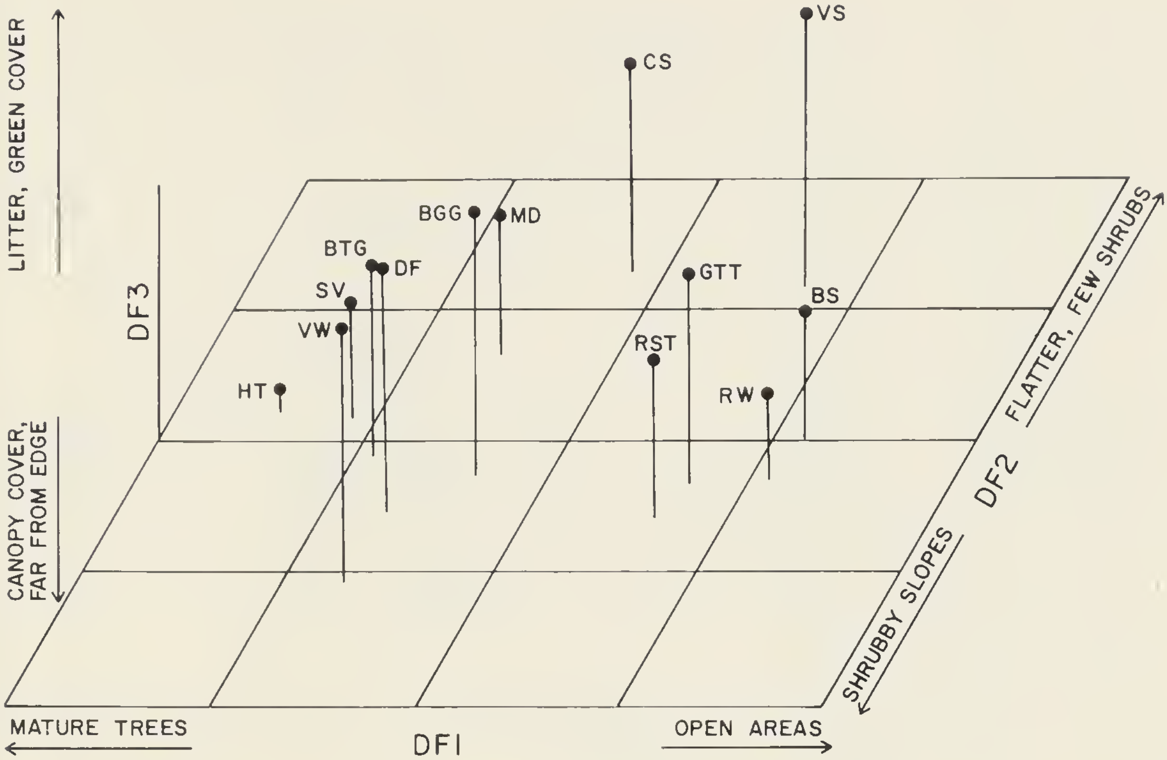

FIG. 1. Ordination of 13 bird species along discriminant axes 1, 2, and 3. See Table 2 for key to species' symbols.

along DF3. Chipping and Vesper sparrows, Virginia's Warbler, Dusky Flycatcher, and Blue-gray Gnatcatcher had the highest scores along this axis, and they preferred high grass, forb, and shrub cover, less canopy cover, or were associated with edges.

Group classification.—PDA correctly assigned 48.9% of the 233 observations to their appropriate groups (Table 4). This is 44.6% better than chance classification (Cohen's Kappa statistic, Wiedemann and Fenster 1978) and is significantly better than could have occurred by random sampling (Z statistic for Kappa, $P < 0.05$). Five species had <50% of their cases correctly classified (Table 4). Three woodland species (Blue-gray Gnatcatcher, Solitary Vireo, and Black-throated Gray Warbler) had positions near the center of the woodland group in discriminant 3-space and overlapped extensively in habitat space with other species (Figs. 1 and 2). Black-throated Gray Warblers were frequently misclassified as Virginia's Warblers, Blue-gray Gnatcatchers, Mourning Doves, or Hermit Thrushes. Blue-gray Gnatcatcher observations were misclassified most as Virginia's Warbler, Mourning Dove, or Black-throated Gray Warbler observations. Solitary Vireos were often misclassified as Hermit Thrushes, Black-throated Gray Warblers, or Blue-gray Gnatcatchers. High misclassification rates for these species suggest a high degree of ecological similarity with the species they were misclassified as regarding the 17 habitat

TABLE 4

CLASSIFICATION MATRIX FOR 13-GROUP DISCRIMINANT ANALYSIS

Actual group	Predicted group membership (%)												
	MD	DF	RW	HT	BGG	SV	VW	BTG	GTT	RST	VS	CS	BS
MD[a]	50.0[b]			14.3	7.1	7.1	7.1	7.1			7.1		
DF		63.6				18.2	9.1		9.1				
RW			72.2	5.6						5.6	5.6		11.1
HT	10.0			50.0		10.0		30.0					
BGG	10.0	5.0			45.0		20.0	10.0	5.0			5.0	
SV				30.8	15.4	30.8		15.4				7.7	
VW		6.7			13.3		66.7	13.3					
BTG	14.3			10.7	17.9	7.1	17.9	25.0				7.1	
GTT			10.0		13.3		10.0		40.0	3.3	3.3		20.0
RST	5.0	5.0	40.0		10.0		10.0		10.0	15.0			5.0
VS					5.9						76.5	5.9	11.8
CS	22.2							5.6			22.2	50.0	
BS			5.3						5.3	5.3	5.3		78.9

[a] See Table 2 for symbols of bird species.
[b] Percentage of correctly classified cases for each species lies along the diagonal.

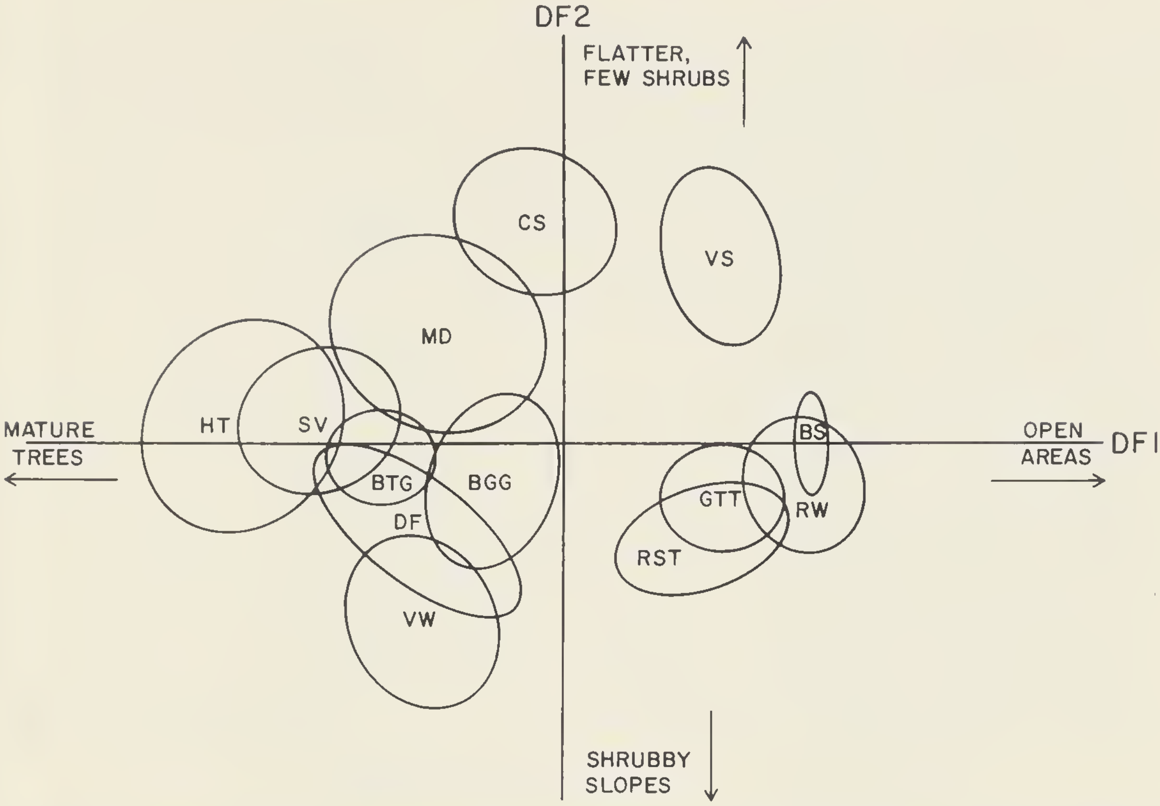

FIG. 2. Ninety-five percent confidence ellipses for the bivariate means of 13 bird species based on discriminant functions 1 and 2. See Table 2 for key to species' symbols.

variables selected by the DDA. Birds of open areas, such as Rufous-sided Towhees, were most frequently misclassified as Rock Wrens; Green-tailed Towhees were most frequently misclassified as Brewer's Sparrows. These species were all close to one another in discriminant 3-space (Fig. 1).

Habitat relationships and habitat-niche breadth.—The habitat-niche (Smith 1977) of each species was compared to that of other species by comparing distances (the Mahalanobis distance) between group centroids in multivariate habitat space. There was a significant difference ($P < 0.05$) in habitat-niche between 74 of the 78 species pairs (Table 5). Large F values correspond to large differences between species in multivariate space and indicate segregation in habitat space. Smaller F values suggest less separation in habitat space. Virginia's Warbler-Dusky Flycatcher ($F = 2.10$) showed less separation, for example, than did Black-throated Gray Warbler-Rock Wren ($F = 10.58$). Species pairs that overlapped considerably (nonsignificant F values) included Solitary Vireo-Hermit Thrush, Green-tailed Towhee-Rufous-sided Towhee, Brewer's Sparrow-Rufous-sided Towhee, and Brewer's Sparrow-Green-tailed Towhee. The sparrow and two towhees were often found in natural openings or chained areas where territories were adjacent or appeared to overlap. Solitary Vireo and Hermit Thrush were frequently found in similar woodland habitats where

TABLE 5

SIGNIFICANCE LEVELS (*F* VALUES) FOR PAIRWISE CONTRASTS BETWEEN 13 SPECIES OF BIRDS BREEDING IN NORTHWESTERN COLORADO

	MD	DF	RW	HT	BGG	SV	VW	BTG	RST	GTT	CS	BS
DF[a]	4.29[b]											
RW	7.41	7.39										
HT	3.06	3.69	10.16									
BGG	2.72	3.21	7.44	5.23								
SV	2.96	3.03	9.54	NS[c]	3.25							
VW	4.42	2.10	7.91	4.66	2.14	3.72						
BTG	2.59	3.44	10.58	3.15	2.16	2.09	2.23					
RST	5.25	4.87	2.21	7.79	3.69	6.85	4.29	6.61				
GTT	5.92	5.29	3.27	9.67	3.67	8.21	5.93	8.93	NS			
CS	2.48	4.74	6.95	5.53	4.38	4.85	6.66	5.00	6.03	6.57		
BS	6.55	7.79	1.87	10.13	6.11	8.91	8.51	10.05	NS	NS	6.47	
VS	5.67	6.44	5.29	10.10	5.31	7.53	8.35	8.53	4.71	3.98	2.90	3.40

[a] See Table 2 for symbols of bird species.
[b] Each F has 17 and 204 degrees of freedom and corresponds to a significance test for the Mahalanobis distance between species.
[c] NS = not significant ($P > 0.05$).

the trees were large, percentage canopy cover was high, and some dead trees were present.

Ninety-five percent confidence ellipses graphically illustrate habitat relationships among the 13 species (Fig. 2). Such ellipses are functions of the variance and covariance of discriminant scores for DF1 and DF2 and will contain the true mean for each species in discriminant 2-space 95% of the time. Some species and species-groups were clearly segregated within the forest type. For example, species that occupied open areas were distinct from the woodland species, and Vesper Sparrow habitat space was well-separated from that of all other species. At least some overlap existed for all other species. In open areas, the greatest overlap occurred between the two towhees and between Brewer's Sparrow and Rock Wren. In woodlands, Hermit Thrush and Solitary Vireo overlapped considerably, suggesting selection for similar habitats. Black-throated Gray Warbler and Dusky Flycatcher each overlapped with five other species, reflecting their central positions in woodland habitat space. Chipping Sparrow was well segregated from the other woodland species along DF2, preferring flatter habitats where shrubs were smaller and less diverse.

As the variance of DF1 and DF2 is a component of the confidence ellipses, these may be thought of as measures of variability in resource use, or as measures of habitat-niche breadth (Pianka 1974). The larger the confidence ellipse, the more variable the species is in resource use. Mourning Dove and Hermit Thrush had the largest confidence ellipses, indicating wide latitude in habitat selection regarding the dimensions described by DF1 and DF2. Brewer's Sparrow had the smallest confidence ellipse, suggesting a narrow range of variability along DF1 and DF2. This species had an especially narrow habitat-niche breadth along DF1, reflecting its habit of nesting in large, monotypic stands of sagebrush. Blue-gray Gnatcatcher, reported in other studies as being a habitat generalist (James 1971, Whitmore 1975), had an intermediate habitat-niche breadth in pinyon-juniper.

Two group DDA: habitat associations.—Species breeding in chainings or natural openings within pinyon-juniper woodlands were positively associated with measures of shrubbiness, openness, percentage log cover, small trees, distance from a habitat edge, and slope (Table 6). Coefficients with the largest positive values for Vesper Sparrow were shrub density (SHRBDEN) and openness (BITZERO), whereas the highest negative values were for shrub dominance (SHRBDOM) and distance from an edge (EDGDIST). Vesper Sparrows could be expected to have high positive scores along this discriminant axis since they were found near edges, and in areas of little to moderate slope characterized by dense, small shrubs, and low shrub diversity. These findings agree with those of Best

TABLE 6

SUMMARY OF THE TWO-GROUP DISCRIMINANT ANALYSES

Variables	Standardized discriminant function coefficients[a]												
	MD	DF	RW	HT	BGG	SV	VW	BTG	GTT	RST	VS	CS	BS
CANHT	–	–	–	–	–	0.49	–	–	−0.71	−0.58	–	–	–
GRNDSP	–	–	–	–	–	–	–	–	–	−0.40	–	0.45	–
PGCOVER	–	–	–	–	–	–	–	−0.43	–	–	–	0.44	–
PBARE	–	−0.50	–	–	–	–	–	–	–	–	–	–	–
PLITTER	–	−0.45	–	–	–	–	0.34	–	–	–	–	–	–
PCANOPY	–	–	–	–	–	–	–	1.00	–	–	−0.36	–	–
PLOG	–	–	0.39	–	–	–	–	–	0.40	–	−0.37	–	–
PDEADTR	0.80	–	–	–	–	–	–	–	–	–	–	–	–
BITPL	–	–	–	0.34	–	–	–	–	–	–	–	–	–
BITJL	–	–	−0.55	–	–	–	–	–	–	–	–	–	–
BITOL	–	–	–	–	–	–	0.46	−0.28	–	–	–	–	–
BITPD	–	–	–	0.25	–	–	–	–	–	–	–	–	–
BITJD	−0.50	–	–	–	–	–	–	–	–	–	–	–	–
BITDEAD	–	–	–	–	0.40	–	−0.31	–	–	–	–	–	–
BITPH	0.31	–	–	–	–	–	–	−0.28	–	–	–	–	–
BITHALF	–	–	–	−0.27	–	–	–	–	–	–	–	–	–
BITZERO	–	–	–	–	–	–	–	–	–	–	0.44	–	0.68

TABLE 6
CONTINUED

Variables	Standardized discriminant function coefficients[a]											
	MD	DF	RW	HT	BGG	SV	VW	BTG	GTT	RST	VS	CS	BS
DENSTYA	–	–	0.30	–	–	–	–	−0.31	–	–	–	0.32	–
DENSTYB	–	–	–	–	0.48	–	–	–	–	–	–	–	–
DENSTYC	0.35	–	–	–	–	–	–	–	–	–	–	–	–
DENSTYE	–	0.42	–	0.88	−0.52	0.63	–	−0.61	–	–	–	−0.40	–
DENSTYF	−0.43	–	–	−0.52	–	–	–	–	–	–	–	–	
DENSTYG	0.65	–	–	–	–	–	–	–	–	–	–	–	–
SHRBHT	–	–	–	–	–	–	–	–	–	0.41	–	–	–
SHRBDIM	–	–	–	–	–	–	–	–	–	–	–	−0.30	0.27
SHRUBSP	–	–	–	–	0.81	–	0.36	–	0.72	–	−0.21	−0.46	−0.23
SHRBDEN	–	–	–	–	–	–	–	–	–	–	1.00	–	–
SHRBDOM	–	0.36	–	–	–	–	–	–	–	–	−0.77	–	–
EDGDIST	–	−0.39	–	0.47	–	–	–	–	–	0.40	−0.50	–	0.31
SLOPE	−0.42	0.68	0.40	–	–	–	0.53	0.38	−0.25	–	−0.31	–	−0.46
ALT	–	0.34	−0.92	–	–	–	–	–	–	–	–	–	–
EWDIREC	–	–	–	–	–	–	–	–	–	–	0.39	–	−0.37

[a] Coefficients indicate relative contributions of habitat variables to discriminant functions comparing nonoccupied habitat to habitat occupied by each species.
[b] See Tables 1 and 2 for descriptions of habitat variables and key to bird species' symbols.

(1972) who found Vesper Sparrows in sagebrush-grassland associations; however, in the Sierra Nevada, Verner and Boss (1980) reported Vesper Sparrows being associated with early successional stages lacking shrubs. In Montana, Reed (1986) also found Vesper Sparrows in a shrubless grassland, but as in this study, they were found where the vegetation was short and dense, and they avoided areas where vegetation was tall and patchy.

Rufous-sided Towhees were positively associated with distance from a habitat edge (EDGDIST) and large shrubs (SHRBHT). They were negatively associated with canopy height (CANHT) and ground species richness (GRNDSP). This matches the presence of towhees in shrubby habitats far from edges where average canopy height and the number of ground species was low. In Arkansas, Rufous-sided Towhees were birds of open-country habitats (James 1971), and in Missouri, they were influenced by litter coverage and woody stems <2.5 cm dbh (shrubs and saplings) (Kahl et al. 1985). Other studies also document the dependence of Rufous-sided Towhees on a well-developed shrub understory (Shugart and James 1973, Nolan 1963, Davis and Savidge 1971).

Green-tailed Towhees selected habitats on the basis of shrub species richness (SHRBSP) and percentage log cover (PLOG). They were negatively associated with canopy height (CANHT) and slope (SLOPE). Whereas canopy height was unimportant and shrubs were important to both towhees, Rufous-sided Towhees were influenced by large shrubs and Green-tailed Towhees were influenced by shrub species richness. Green-tailed Towhees were attracted to small patches of dense shrubs in the Sierra Nevada (Verner and Boss 1980); and in Washington and Oregon, Green-tailed Towhees were "low to moderate shrub-form" nesters (Thomas 1979). In this study, they were especially common in sagebrush-dominated openings within pinyon-juniper woodland. Green-tailed Towhees are frequent inhabitants of sagebrush habitats and are considered sagebrush near-obligates (Braun et al. 1976).

Rock Wrens selected areas with high percentage log cover (PLOG), density of small trees (DENSTYA), and slope (SLOPE). They were negatively associated with live junipers (BITJL) and high altitude (ALT). This association matches the Rock Wren's presence in low-altitude chainings where log cover (slash) and small tree density were high. Rock Wrens are characteristic of early successional habitats (Bent 1948, Thomas 1979) and are often associated with rocky outcrops, but may also use slash piles in pinyon-juniper chainings (Sedgwick and Ryder 1986).

Brewer's Sparrows selected open (BITZERO) habitats with large shrubs (SHRBDIM) and were typically found far from edges (EDGEDIST). Their habitats were also characterized by small slopes (SLOPE) and low shrub species richness (SHRBSP). Brewer's Sparrows occurred in sagebrush-grasslands in Montana (Best 1972) and were characteristic of large sagebrush openings in pinyon-juniper woodland in the Piceance Basin. Wiens and Rotenberry (1981) found Brewer's Sparrows at their highest densities in open, flatland habitats and where shrub diversity was low, as in Colorado. Other habitat associations of Brewer's Sparrows include positive correlations with shrub cover, bare ground, and forb cover, and negative correlations with grass and litter cover and the amount of rockiness (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981).

Woodland species were strongly associated with high canopies, high percentage canopy cover, live and dead pinyons, and high tree densities. Solitary Vireos selected habitats on the basis of canopy height (CANHT) and large tree density (DENSTYE), and they were associated with only the most mature stands of pinyon-juniper. In the Sierra Nevada, Solitary Vireos used shrubby understories and low to intermediate canopy cover (Verner and Boss 1980), and they used intermediate-stage conifer communities in the Blue Mountains of Oregon and Washington (Thomas 1979). This species may be more of a generalist regionwide than indicated by the results of any particular study.

Hermit Thrushes also used mature stands of pinyon-juniper, being favored by large trees (DENSTYE), and by live (BITPL) and dead (BITPD) pinyons. They selected interior woodland habitats and avoided sites near edges (EDGDIST). This species is typically associated with mature, forested habitats and forest interiors (Thomas 1979).

Black-throated Gray Warbler habitat was distinguished from nonhabitat by relatively steeper slopes (SLOPE), and higher canopy cover (PCANOPY). Areas with steep slopes are typically not chained, and these situations were favored by Black-throated Gray Warblers. Conversely, Verner and Boss (1980) report some preference for areas with low percentage canopy coverage, and Thomas (1979) describes Black-throated Gray Warblers as nesters of "0.3 to 1.2 m high shrub-form habitats" within the conifer zone. Apparently, this species is flexible in its choice of canopy and shrub coverage.

Dusky Flycatchers selected habitats on the basis of shrubby slopes (SHRBDOM, SLOPE) where large trees (DENSTYE) were present. They were also influenced by ground cover (PBARE, PLITTER), and preferred edge situations (EDGDIST). Dusky Flycatchers are typically associated with shrubby habitats with scattered trees or occur in open conifer forest (Grinnell et al. 1930, Sumner and Dixon 1953).

Virginia's Warblers showed a strong relationship with steep slopes (SLOPE), litter cover (PLITTER), live Gambel's oak (BITOL), and shrub species richness (SHRBSP). They were negatively associated with dead trees (BITDEAD). In the Piceance Basin, they were found almost exclusively in Gambel's oak chapparal or in oak-covered draws within pinyon-juniper woodland. Various shrub-form associations are favored by Virginia's Warblers throughout the West, including mountainmahogany, snowberry, willow (*Salix* spp.), sage, and plum (*Prunus*) (Bent 1953).

Chipping Sparrows selected a more open habitat where small trees (DENSTYA), ground species richness (GRNDSP), and ground and green cover (PGCOVER) were above average. They were negatively associated with shrub size (SHRBDIM), large tree density (DENSTYE), and shrub species richness (SHRBSP). Chipping Sparrows were characteristic birds of open country in Arkansas (James 1971) and were associated with small shrub patches in the Sierra Nevada (Verner and Boss 1980).

Mourning Doves were associated with moderate slopes and areas where trees were large (DENSTYG) and dead and dying trees (PDEADTR) were present. In the Sierra Nevada of California, this species preferred stands with low percentage canopy cover (Verner and Boss 1980). Mourning Doves are habitat generalists (Stauffer and Best 1980) occurring in a wide variety of habitat types.

Blue-gray Gnatcatchers were positively associated with 3 habitat variables—shrub species richness (SHRBSP), small trees (DENSTYB), and dead trees (BITDEAD). Both James (1971) and Whitmore (1975) found this species to be a habitat generalist showing wide latitude in habitat use. Similarly, this species was observed in all forest habitats in Missouri, and habitat selection seemed random (Kahl et al. 1985). In this study, their broad latitude in habitat selection is reflected by their central position in woodland habitat space and their association with both shrubby, open chainings (SHRBSP and DENSTYB) and with mature pinyon-juniper (BITDEAD). In Tennessee, Anderson and Shugart (1974) found Blue-gray Gnatcatchers to be associated with understory biomass.

CONCLUSIONS

Two broadly defined groups of birds can be identified in this study: woodland species and open-area species. Hermit Thrushes, Solitary Vireos, and Black-throated Gray Warblers, for example, overlapped extensively in woodland habitat space and were generally dependent on forest overstory, being associated with late-successional stages of the pinyon-juniper type. All would be especially susceptible to chaining. Similarly, Green-tailed Towhees, Rufous-sided Towhees, and Rock Wrens showed extensive overlap and shared habitat associations in open-area habitat space. These species are early successional species and would benefit from chaining.

Species with extreme values along the discriminant axes were also identified; these species were most obviously distinct from all other species and their habitat preferences were most easily described. Virginia's Warblers, for example, preferred shrubby, oak-covered slopes with high grass, forb, and shrub cover. Chipping Sparrows preferred edge habitats intermediate between woodlands and openings, and Hermit Thrushes were found only in the most mature woodland situations far from habitat edges. Vesper Sparrows favored small shrubs in relatively flat areas. Habitat-niche exclusiveness is reflected in the high rates of correct classification of cases for these species. Other woodland species (Solitary Vireo, Black-throated Gray Warbler) and species of open areas (Green-tailed Towhee, Rufous-sided Towhee) occupied central positions in woodland and open-area habitat space, respectively. Habitat-niches of these species were not well segregated, and their habitat preferences were less unique.

The two-group DDA provided greater resolution and identified habitat relationships more specifically. Associations of species with specific habitat variables suggest varying susceptibilities to habitat change. The association of Hermit Thrushes, for example, with mature woodland and great distance from a habitat edge suggests that they would be especially susceptible to forest fragmentation (cf. Ambuel and Temple 1983). Dusky Flycatchers, on the other hand, were associated with edges and a diverse understory of large shrubs, and would benefit from the creation of small openings in the woodland overstory. Vesper and Brewer's sparrows both were associated with stand openness and would benefit from the creation of relatively large openings in pinyon-juniper woodland. Both the Green-tailed and Rufous-sided towhees were favored by the presence of shrubs, and habitat alterations creating shrublands would benefit these species. Management actions that change the structure or coverage of the vegetation should consider those variables that loaded highly on the discriminant functions and that most strongly influenced habitat selection.

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